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DISTRIBUTIONAL AND PHYLOGENETIC STUDIES ON INDIAN FOSSIL MAMMALS. IV

THE PHYLOGENY OF THE INDIAN SUIDAE AND THE ORIGIN OF THE HIPPOPOTAMIDAE

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THE PHYLOGENY OF THE INDIAN SUIDAE

During the middle and later portions of the Tertiary period, India was a great center for the adaptive radiation of the Suidae. The fossil remains of pigs are numerous in the Siwalik deposits of the northern Punjab, and they represent a variety of types indicative of the phylogenetic plasticity of the suid group. Here, in one locality, in a series of deposits ranging in age from Upper Miocene to Lower Pleistocene, may be found almost the complete phylogenetic history of the Suidae, from the most primitive, undifferentiated types to the very advanced, highly specialized genera. The following remarks will constitute a brief review of the Indian fossil Suidae, as found in the Siwalik Series, with especial emphasis on their relation to the general phylogenetic history of the group.

PREVIOUS STUDIES ON SIWALIK SUIDAE

Of course the first serious student of fossil pigs from the Siwalik beds was Hugh Falconer, the founder of Vertebrate Palaeontology in India. In the 'Fauna Antiqua Sivalensis,' part 8, published in 1847, several genera and species of Suidae were named and illustrated. Falconer did not, however, contribute anything in the manner of a survey or a systematic study of the Indian fossil Suidae that he had named.

In 1884, Richard Lydekker published his 'Siwalik and Narbada Bunodont Suina' in the 'Palaeontologica Indica.' This was a detailed monograph on all of the Indian fossil pigs known at the time, and although Lydekker did not discuss the phylogeny of the Suidae, he did consider, in his descriptions of the various species of Siwalik suids, the probable relationships of these forms to each other and to other pigs.

In 1899, Hans Stehlin published 'Geschichte des Suiden Gebisses,' a lengthy monograph on the evolution and structure of the teeth in the

Suidae. In this work were included descriptions of the teeth of the various genera and species of Siwalik pigs.

Dr. Guy E. Pilgrim brought out, in 1926, his monograph entitled 'The Fossil Suidae of India.' This was a complete review of the species known to Lydekker, and in addition Pilgrim described several new genera and a number of new species on the basis of specimens discovered by himself in the Punjab. Pilgrim's explorations in the Kamlial and Chinji horizons of the Lower Siwaliks, faunal zones unknown to Lydekker, greatly augmented the number of species and genera of suids from the Siwaliks. In this monograph, Pilgrim presented a large chart that diagramed the phylogenetic classification of the Suidae.

Pilgrim's phylogenetic diagram for the Suidae is noteworthy because of the detail in which it is carried out, based as it is on his important and careful studies of the Siwalik pigs in the London and the Calcutta museums. It would seem to me, however, that this phylogeny as presented by Pilgrim, is unduly complex, due to the fact that he has placed great weight on rather small differences of dental structure in his formulation of a classification for the group under consideration. In making this criticism I follow the lead of Dr. Matthew, who expressed a similar opinion in 1929, in the following manner.

"Doctor Pilgrim has recently monographed the Indian Suidae, but his methods appear to me to place too much weight upon one or two unsupported differentiation characters, allowing not enough for individual variation, and resulting in an extraordinarily complex arrangement which would be far more complex if the same methods were applied to *all* the Old and New World suillines, instead of only to the Indian groups."[1]

In the following pages there will be presented brief discussions of the several genera of Siwalik Suidae. Species will be considered incidentally, where they may come into the discussion. Finally, a phylogeny for the Siwalik pigs will be outlined, which may be compared directly with Pilgrim's phylogeny of 1926.

A Discussion of the Indian Suidae

In the discussion to be offered below the Suidae are considered as divisible into several phylogenetic groups or branches. Each of these groups is supposed to be a phylogenetic unit, and as such each is discussed. The Siwalik Suidae have been divided in the following manner.

[1]Matthew, W. D. 1929. Bull. Amer. Mus. Nat. Hist., LVI, p. 455.

GROUP I—*Palaeochoerus*
GROUP II—*Listriodon*
GROUP III—*Conohyus–Sivachoerus–Tetraconodon*
GROUP IV—*Dicoryphochoerus–Sus–*[*Phacochoerus*]
Propotamochoerus–Potamochoerus
Hyosus–Sivahus–Hippohyus
GROUP V—*Lophochoerus*
GROUP VI—*Sanitherium*

GROUP I

PALAEOCHOERUS

Although the remains of *Palaeochoerus* are not common in the Siwalik Series, still they are present to a degree sufficient to establish the genus as having lived through Lower and Middle Siwalik times. Here is an example of the persistence of a primitive, ancestral form to a period much later than its typical time of phylogenetic development, so that it exists side by side with its specialized descendants.

Palaeochoerus may be considered as close to the stem form for all of the Suidae, and it first appears in the Oligocene of Eurasia. It is structurally primitive, being of small size, with an unspecialized type of skull and with bunodont, simple cheek teeth. From *Palaeochoerus* the later Tertiary pigs developed along several lines of adaptive radiation, characterized by a considerable diversity of skull form and of tooth structure.

The species of *Palaeochoerus* in the Siwalik Series are quite similar to the typical *Palaeochoerus* of the Eurasiatic Oligocene, so we are justified in the conclusion that the genus persisted on from the Oligocene into the Middle Pliocene in India, without undergoing any appreciable evolutionary changes. Thus *Palaeochoerus* in India is a primitive suid, structurally ancestral to the advanced genera with which it is contemporaneous.

GROUP II

LISTRIODON

The genus *Listriodon* is very abundant through the Lower Siwaliks, and it persists on into the lower portions of the Middle Siwaliks. This form must have split off at an early date from the primitive *Palaeochoerus* type of ancestor, for it is specialized in an aberrant manner, quite separated from the more normal kinds of pigs.

Listriodon pentapotamiae the most common species of the genus in India, is closely related to *Listriodon splendens* of Europe and to *Listriogon mongoliensis* of Asia. It is characterized by its very lophodont molar teeth, which in structure closely resemble the teeth of a tapir, by

its heavy upper canines and its laterally directed lower canines. The genus *Listriodon* is also characterized by its rather long, low skull, in which the orbit is set back behind the third molar making the preorbital portion extraordinarily long for a suid of such a geologically early development.

In the Kamlial zone of the Lower Siwaliks there is a primitive, bunodont *Listriodon* which gives us a clue as to how the transition from the more normal suid to the listriodont type took place. This form is the species, *L. guptai*. It is characterized by its small size and its bunodont molars, in which the cross crests, so typical of the more advanced listriodonts, are as yet imperfectly developed.

Group III

Conohyus–Sivachoerus–Tetraconodon

The genus *Conohyus*, a suid of relatively primitive form, is closely related to the genus *Hyotherium*, found in Europe. *Hyotherium* is obviously a fairly direct descendant from *Palaeochoerus*, showing advances over the primitive Oligocene genus, mainly in its larger size, its somewhat more elongated skull, and its slightly more advanced molar teeth. Now *Conohyus* is quite similar to *Hyotherium* in a majority of its features, but it is distinctive especially by reason of its greatly enlarged third and fourth premolars. There are also certain skull characters of *Conohyus* that set it apart, as has been set forth in a recent paper descriptive of the first known skull from the Siwalik Series.[1] Features of special interest are the deeply expanded zygomatic arch, which projects below the occlusal line of the cheek teeth, and the rather elongated preorbital portion. In this discussion, however, we are particularly interested in the evolution of the cheek teeth.

Conohyus is a Lower and Middle Siwalik genus. In the Middle and Upper Siwaliks are two genera that are undoubtedly derived from *Conohyus*. These are *Sivachoerus* and *Tetraconodon*, suids of gigantic size in which the last two premolars are greatly enlarged. *Sivachoerus* is the more generalized of the two, for the development of this form from *Conohyus* has been accomplished mainly by an increase in size and by a certain amount of complication of the cheek teeth. The last two premolars are large, but proportionately they are not very much different from the same teeth in *Conohyus*. *Tetraconodon*, on the other hand, is marked not only by its great actual increase in size over the ancestral type, but also by a very great *proportional* increase in the last two pre-

[1]Colbert, E. H. 1933. Amer. Mus. Novitates, No. 621.

molars, so that they have become really gigantic as compared to the premolars ahead of them and the molars behind them. The increase in size, both actually and proportionally, in *Tetraconodon*, has been accompanied by the development of a heavily rugose surface on these teeth.

We see that the evolution of *Sivachoerus* and *Tetraconodon* from *Conohyus* has followed the same general trend in both of the advanced genera, but that the development of *Tetraconodon* has been much more rapid and has advanced to more specialized ends than is the case with *Sivachoerus*. Therefore we may imagine these two genera as the terminal members of a dichotomous branching from the ancestral *Conohyus* type.

Group IV

Dicoryphochoerus–Sus–Phacochoerus

Propotamochoerus–Potamochoerus

Hyosus–Sivahyus–Hippohyus

This group is composed of a variety of genera rather closely related to each other, but which, nevertheless, represent a fairly wide range of adaptive radiation. These are the advanced and what we might call the "normal" suids. They are typified by the elongation of the skull, the complication of the cheek teeth, and by the various development of fighting tusks.

The genus *Dicoryphochoerus*, described by Pilgrim, may be considered as approximating the stem, or perhaps more properly the central branch of this phylogenetic group. *D. haydeni*, a species found in the Chinji zone of the Lower Siwaliks, would seem to represent the most primitive species of the genus, and consequently it would seem to be typical of the ancestor of this entire phylogenetic group. It is a medium-sized suid in which the cheek teeth have not developed the complexities so characteristic of the later members of this group. That is, the accessory conules so abundantly developed in the more advanced genera are, in this form, conspicuously absent, and the third molar is relatively short.

The later species of *Dicoryphochoerus* are considerably advanced over *D. haydeni*, both in size and in complexity of the cheek teeth. The species *D. titan* attains a size that might be called almost gigantic. In the phylogenetic advance of this genus, however, the tendency of the cheek teeth is to retain their primitive shortness, rather than to lengthen anteroposteriorly, as is the case with the genus *Sus*. Even *D. titan*, the most advanced species of the genus, has a third molar that is relatively

quite short, in spite of the degree of complexity that marks its crown pattern.

The genus *Sus* would seem to have branched out from the primitive *Dicoryphochoerus haydeni*. *Sus* has paralleled *Dicoryphochoerus* in its evolutionary history, but whereas the teeth of *Dicoryphochoerus* are short, the teeth of *Sus* become greatly elongated. These differences of phylogenetic expression are shown in the skulls of the two genera, correlative with their development in the teeth. The skull of *Dicoryphochoerus* is comparatively short and deep, whereas the skull of *Sus* is very long, with an elongated preorbital portion.

One of the Siwalik species, namely *Sus falconeri*, would seem to be more or less in a direct line leading to the genus *Phacochoerus*, now found in South Africa. *Sus falconeri* is quite a large pig in which the skull and the teeth are greatly elongated. The orbit of this Siwalik species is set far back, behind the last molar, a character foreshadowing the extreme posterior placement of the orbit in the wart hog. The glenoid of the Siwalik form is raised, and as a corollary to this the ascending ramus of the mandible is high. These again are characters found in *Phacochoerus*. Then again, the jugal of *Sus falconeri* is rather heavy, which would seem to be a development in the line of *Phacochoerus*. Turning to a consideration of the mandible, we see that the symphysis of the Siwalik species is heavy and long, much as it is in the African genus. The third molar of *Sus falconeri* is very suggestive of that tooth in *Phacochoerus*, because it is greatly elongated, and this elongation has caused the talon and the talonid to become divided into a longitudinal series of lateral and median conules, which when worn form a pattern that shows incipient stages toward the wart-hog pattern. Of course, *Phacochoerus* is a highly specialized pig and it shows many characters, such as the extreme reduction of the cheek dentition anterior to the last molar, the posterior, high orbit and the like, that are not found in *Sus falconeri*. Recently some Pleistocene phacochoeres have been described from South Africa by van Hoepen,[1] and some of these, notably the genus *Kolpochoerus*, help to bridge the gap between *Sus falconeri* and *Phacochoerus*. Thus it would seem reasonable to suppose that *Sus falconeri* of the Siwaliks is a species close to the point where the phylogenetic branch of phacochoeres split away from the normal pigs.

Another branch from the general *Sus* stem would seem to be that of the *Hyosus–Hippohyus* line. This branch is represented in ascending

[1]Van Hoepen, E. C. N., and van Hoepen, H. E. 1932. 'Paleontologiese Navorsing van die Nasionale Museum, Bloemfontein,' II, Pt. 4, pp. 39–62.

order by the genera *Hyosus* and *Sivahyus* (possibly synonymous with each other) and by the genus *Hippohyus*. It was characterized by the development in the molar teeth of a very complex system of cones and conules, which when worn form an exceedingly complicated enamel pattern. Moreover, the teeth became quite hypsodont. On the other hand, the skull retained a primitive feature in that it remained rather short with a comparatively centrally placed orbit, and a rather short preorbital portion. The skull was specialized in the development of very heavy zygomatic arches. Although, at first glance, the teeth of *Hippohyus* would seem to be extraordinarily different from the usual pig tooth, they may be resolved, when subjected to a careful analysis, to the pattern characteristic of *Sus*. This shows the basic relationship of *Hippohyus* to *Sus* and it shows that the specializations in the former genus are those of degree rather than of kind.

Hyosus and *Sivahyus* are small genera with complexly folded enamel in the molars. They are directly ancestral to *Hippohyus*, which differs from them mainly by virtue of its greater size and its more hypsodont teeth.

Finally we come to a consideration of the genera *Propotamochoerus* and *Potamochoerus*. I cannot agree to Pilgrim's interpretation that these genera are widely divergent from *Dicoryphochoerus* and *Sus*. It would seem to me that they are, on the contrary, very close to the *Sus* line, and that their differences from the *Sus* branch of development are for the most part of a minor character. Pilgrim made a great point of the differences in the last lower premolar in these two groups. In the *Potamochoerus* line the last lower premolar consists of a single cone, with sometimes a very minute cone behind it and accessory upon it. On the other hand, in *Dicoryphochoerus* and *Sus* the last lower premolar has the form of a double cone, with the two apices closely appressed and either in line, one behind the other, or slightly oblique, so that the posterior one is somewhat internal to the anterior one. Other differences accompany these distinctions in the premolars. In the *Potamochoerus* group the cheek teeth are on the whole less complicated than they are in the *Sus* group, and likewise, the skull in the former group tends to be slightly stockier than it is in the latter group. But these, it seems to me, are not differences of fundamental import. Basically, on the evidence of skulls, jaws and teeth, the two groups of suids under discussion would seem to be very much like each other. Therefore, we may imagine them splitting apart late in the Tertiary period, retaining their similar *heritage* characters, but developing *habitus* characters that set them slightly

apart one from the other. It would seem logical to suppose that this division of the two groups occurred during Lower Siwalik times. *Propotamochoerus salinus* and *Dicoryphochoerus haydeni*, Chinji forms that may be taken as fairly well representative of the most primitive species of the two groups now under consideration, are certainly very much like each other.

Propotamochoerus is like *Potamochoerus*, but it is slightly more primitive in structure. The molar teeth are perhaps a little less complex in the former than they are in the latter, and the third molar is less elongate.

Group V

Lophochoerus

The genus *Lophochoerus* was erected by Pilgrim in 1926 to include some very small supposedly suid jaws from the Lower and Middle Siwaliks. As defined by Pilgrim, this genus is distinguished by its semi-selenodont molar teeth, in which respect it closely resembles the primitive but aberrant European Miocene suid, *Choerotherium*. Pilgrim distinguished this genus from *Choerotherium*, however, by its stout, conical P_4. The manner in which *Lophochoerus* is related to the other suids is a question of some difficulty. Pilgrim has suggested that it is an offshoot from the *Propotamochoerus–Potamochoerus* stem.

Group VI

Sanitherium

Sanitherium is a very small, rather aberrant genus of Siwalik suids, seemingly derived from the *Dicoryphochoerus–Sus* branch of phylogenetic development. It is characterized by its rather elongated molars, having infolded cusps, and by the beaded cingulum around the bases of the cheek teeth.

The accompanying figure presents a chart embodying the above outlined ideas concerning the phylogeny of the Siwalik Suidae. The several phylogenetic groups as presented in the foregoing paragraphs are indicated by branching lines, and the species most typical of them are placed at their proper stratigraphic levels. Only the species that are considered to be of true worth are included in this chart. A number of Pilgrim's species, which are possibly synonyms of the species placed on this chart, are not here included.

It will be noticed that the present phylogenetic chart differs from the chart outlined by Pilgrim in 1926 by its greater simplicity. This

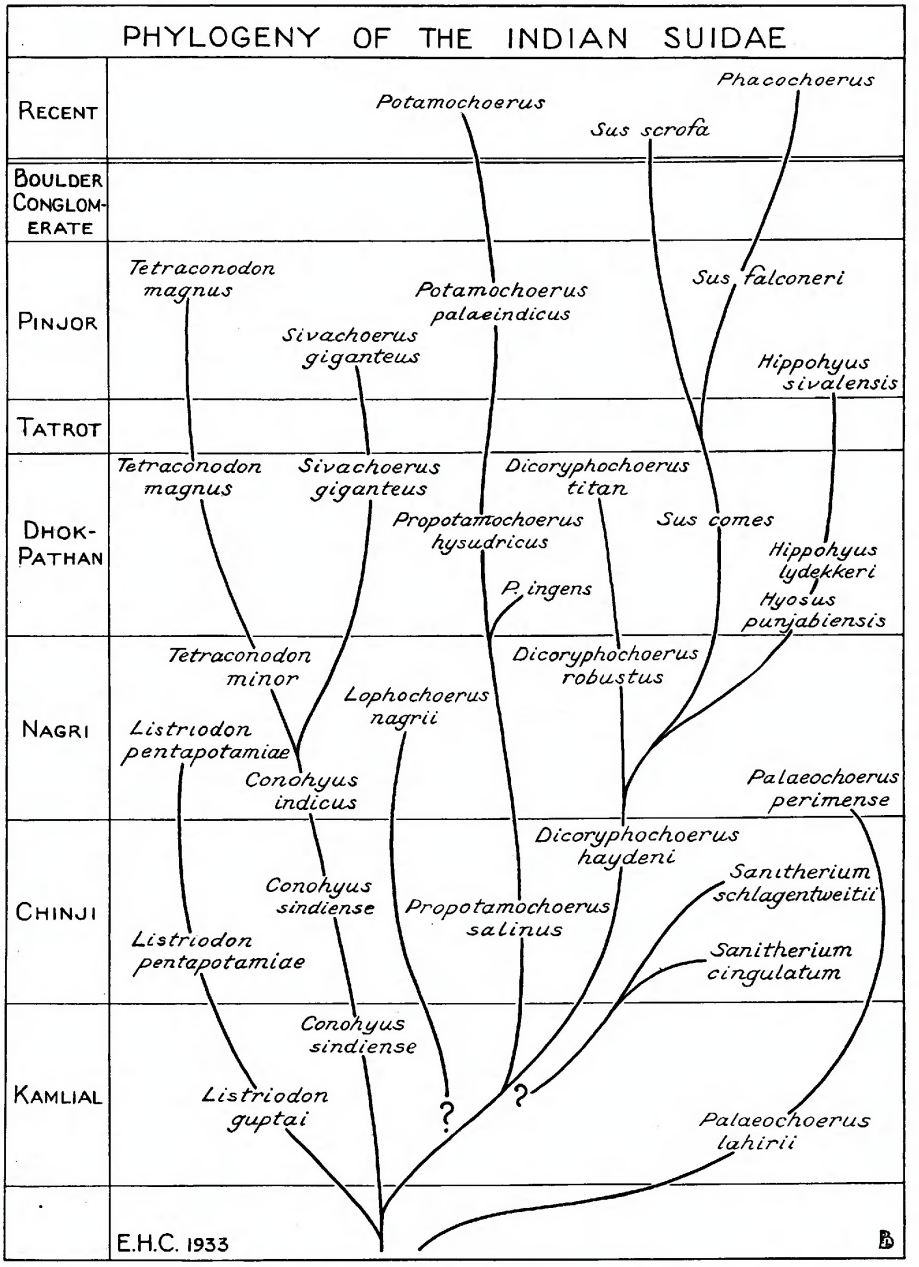

Fig. 1. Phylogeny of the Indian Suidae.

difference is due to certain fundamental differences of thought. Dr. Pilgrim considers the Suidae to be polyphyletic down to the base of the Eocene, but I consider the Suidae to be monophyletic through the earlier portions of the Tertiary period. According to my idea the pigs did not begin their adaptive radiation until some time in the Oligocene.

The Origin of the Hippopotamidae

Three explanations for the origin of the Hippopotamidae have been advanced during the course of the past hundred years. These are listed below.

1.—The Hippopotamidae have been derived from the Suidae, a view advocated by various authors, and recently supported by Matthew.

2.—The opposite theory is the one that would derive the Hippopotamidae from the Anthracotheriidae. This idea was especially supported by Andrews, but before him Falconer and Lydekker, had suggested a relationship between these two families, basing their conclusions particularly on the *Hippopotamus*-like habitus of the anthracothere genus *Merycopotamus*.

3.—A recent theory has been advanced by Miss H. S. Pearson, who would derive the Hippopotamidae from certain Eocene bunodonts, notably *Cebochoerus*.

Good arguments may be elicited in favor of any one of these theories, for there can be found in the genus *Hippopotamus* characteristic pig, anthracotherine, and cebochoerid features. The problem is: how to evaluate this assemblage of characters found in *Hippopotamus*, and to which ones emphasis should be given. Perhaps the problem is beyond solution at the present time, but at least it may be attacked, and the various possibilities presented by it may be carefully considered. Such a procedure will be attempted in the following pages.

Characters of the Groups Under Consideration

First let us turn to a brief review of the diagnostic characters of the Hippopotamidae, of the Anthracotheriidae, of the Suidae, and of *Cebochoerus* (often set apart as a separate family, the Cebochoeridae).

Hippopotamidae

The primitive dental formula is retained except in the modern genus *Hippopotamus*, in which form one incisor, probably the second, is lost. In the more primitive genera the central incisor is of normal size, but in the advanced forms, such as *Hippopotamus*, this tooth is greatly en-

larged. The canines are large, directed vertically, and their surfaces are heavily striated longitudinally. The anterior premolars consist essentially of a single cone. The fourth premolar above and below is more complex, being made up of an outer and an inner cone in the upper tooth, and of two closely appressed lateral cones and a low posterior cone in the lower tooth. The molars are composed in each case of two pairs of trefoils, with the bases of the trefoils directed toward the midline of the tooth. There is no talon nor talonid in the last molars. All of the cheek teeth have well-developed cingula.

The skull in the Hippopotamidae is highly specialized. The orbit is elevated, with a well-developed postorbital bar. The maxilla is expanded above the heavy canine. The occiput is vertical and broad. The glenoid is low, being but little raised above the occlusal line of the molars. The paroccipital processes are short and the bullae are low and only moderately expanded. The basicranial foramina are coalesced around the bulla. The external auditory meatus is long and directed upward. The nasals are expanded at the base.

The mandible is very heavy, with a broad symphyseal region, and with a large, ventrally produced angle.

The body is heavy, and the legs are relatively short. The foot has four functional toes.

ANTHRACOTHERIIDAE

In the anthracotheres there is a full dental formula. The canines are directed vertically and are rather large. The premolars are simple, being composed of a single cone in the anterior members of the series, and of an outer and an inner cone in the fourth upper premolar. The molars are buno-selenodont, the upper ones consisting of four crescentic cusps (with a fifth cusp, the protoconule present in the more primitive forms), and the lower ones consisting of two outer crescentic cusps and two inner conical cusps. There is a well-developed talonid in the last lower molar.

The primitive Eocene anthracotheres have an unspecialized skull, but in some of the more advanced Pliocene and Pleistocene forms the skull becomes highly specialized. The genus *Merycopotamus*, found in the Upper Siwaliks, has an elevated orbit, whereas the more primitive genera do not have the orbit raised. The occiput of the anthracotheres tends to be rather broad, especially in the larger and heavier forms. The glenoid is relatively low. The paroccipital processes are short and the bullae are low and but moderately expanded. The external auditory

meatus is rather short. The basicranial foramina are quite separate in the primitive forms, but in some of the advanced genera, such as *Merycopotamus*, they are coalesced around the bulla—an advanced artiodactyl character.

The mandible is characterized by its shallow horizontal ramus. In *Merycopotamus* the symphysis is very heavy and broad, and the angle is produced ventrally in a manner extraordinarily similar to the ventrally produced angle in the Hippopotamidae.

Merycopotamus is a heavy bodied animal; the more primitive anthracotheres are naturally more slenderly built. The foot is functionally four-toed.

SUIDAE

The full dental formula is retained in the primitive pigs, but in some of the specialized genera there may be a reduction of incisors, premolars, and molars. The canines are almost invariably directed outward, or outward and upward. The cheek teeth are bunodont, and in the more advanced suids there is a strong tendency toward the production of numerous accessory conules. The premolars are rather complicated, so that even in the anterior members of the premolar series there is generally a high cone or two appressed cones, with a low internal shelf in the upper teeth and a low posterior heel in the lower teeth. The last upper premolar usually consists of two outer cones and one inner cone, but the last lower premolar is made up of the characteristic high central cone or cones and the low heel. In the primitive suids the molars consist, each one, of four simple cones, and in the last molars above and below there are simple talons and talonids. Very early, however, in the phylogenetic history of the Suidae there is a very strong tendency toward elongation of the molars, especially the third molar, and the production of numerous accessory conules. The last molar may become extremely long, by a process of lengthening the heel, and the cusps may become quite numerous.

The skull in the Suidae is marked by its tendency to elongate, especially in the preorbital region. This is accomplished not only by a drawing out of the face but also by a backward and sometimes an upward migration of the orbit. The zygomatic arch tends to expand, both laterally and vertically. The glenoid is invariably high, so that the mandibular articulation is raised above the occlusal line. As a corollary to this high glenoid, the paroccipital processes are long, and the bullae are expanded ventrally. The basicranial foramina are coalesced around the

bulla, except in the most primitive suids. The external auditory meatus is long and directed upward. The occiput is narrow, and it overhangs the condyles.

The mandibular symphysis is narrow and the angle is not produced ventrally. The ascending ramus is high.

The body is compact, and the legs are moderately long. There are but two functional toes; the lateral digits, although well developed, do not touch the ground.

CEBOCHOERUS

Cebochoerus is an Eocene artiodactyl from Europe. Although it is primitive in its general aspect, it does show certain well-marked specializations that set it apart as a definitely aberrant form. The full dental formula is retained, at least in the mandible. There is some reason to believe that some of the upper incisors were absent. The upper canine is rather small and vertical, and the lower canine is incisiform and in series with the incisors. Both upper and lower first premolars are specialized to assume the function of canines. The other premolars are simple in the mandible, but in the maxilla the fourth premolar is laterally expanded so that it consists of an outer and an inner cusp. The molars are quadrate above with five cusps, and below they are but slightly elongated and have four cusps. There is a very small talonid in the third lower molar. Accessory cusps and cingula are lacking.

The skull of *Cebochoerus* is short and deep, with the orbit centrally placed. The occiput is vertical and very broad, resembling in this respect, and to a certain degree, the occiput in the anthracotheres or the hippopotamuses. The glenoid is low, being raised but little above the occlusal line, and as an accompaniment to this character the paroccipital processes are short. The bulla is small and the basicranial foramina are separate, as might be expected in a genus of Eocene age. The external auditory meatus is short and extended laterally. The zygomatic arch is rather long, but it is not specialized in any way.

The mandible is very deep, especially in the posterior portion. The symphysis is fairly heavy and the ascending ramus is low and wide.

The skeleton is imperfectly known.

These are the salient characters of the several mammalian groups being considered in connection with the problem of the origin of the Hippopotamidae. Let us now turn to an evaluation of the resemblances and differences between these several types of mammals, in an attempt to discover which of them is most closely related to the Hippopotamidae.

We will first discuss, in a comparative fashion, the resemblances and differences existing between the Hippopotamidae, the Suidae, and the Anthracotheriidae.

A Comparison of the Hippopotamidae, Anthracotheriidae, and Suidae

A.—Dentition

If the *Hippopotamus* molar pattern was derived from the suid molar pattern the following steps were involved.

1.—Coalescence of certain accessory conules with the primary cusps of the suid molar, to form the trefoil of the hippopotamid molar.

2.—Suppression of all superfluous accessory conules.

3.—Shortening of the tooth and the elimination of the heel in the third molar.

If the *Hippopotamus* molar pattern was derived from the anthracotherine molar pattern, this derivation followed the following phylogenetic course.

1.—Transformation of the anthracothere crescents into the *Hippopotamus* trefoils.

It at once becomes apparent that the steps involved in the transformation of an anthracotherine molar into a *Hippopotamus* molar are much simpler than those required for the change of a suid molar into a *Hippopotamus* molar, a fact that favors the view that the Hippopotamidae may have been derived from the anthracotheres.

The manner in which the anthracothere or the suid molars may have been changed into a *Hippopotamus* molar are shown in the accompanying illustration (Fig. 2).

Perhaps it might be well at this point to make a few explanatory remarks regarding the figure illustrative of the discussion now being presented.

Conohyus is chosen as a fairly primitive suid, of a kind that might have been structurally ancestral to the Hippopotamidae. If the Hippopotamidae were derived from the Suidae, they must have sprung from some primitive type of suid, because all of the more advanced pigs trend away from the *Hippopotamus* habitus too definitely to be considered as probable ancestral forms. Even *Conohyus* is probably far too advanced along the suit habitus to constitute a very good ancestral type. It is used here because it is rather primitive, and because it is known from complete dentitions, a skull and a mandible. *Merycopotamus* is

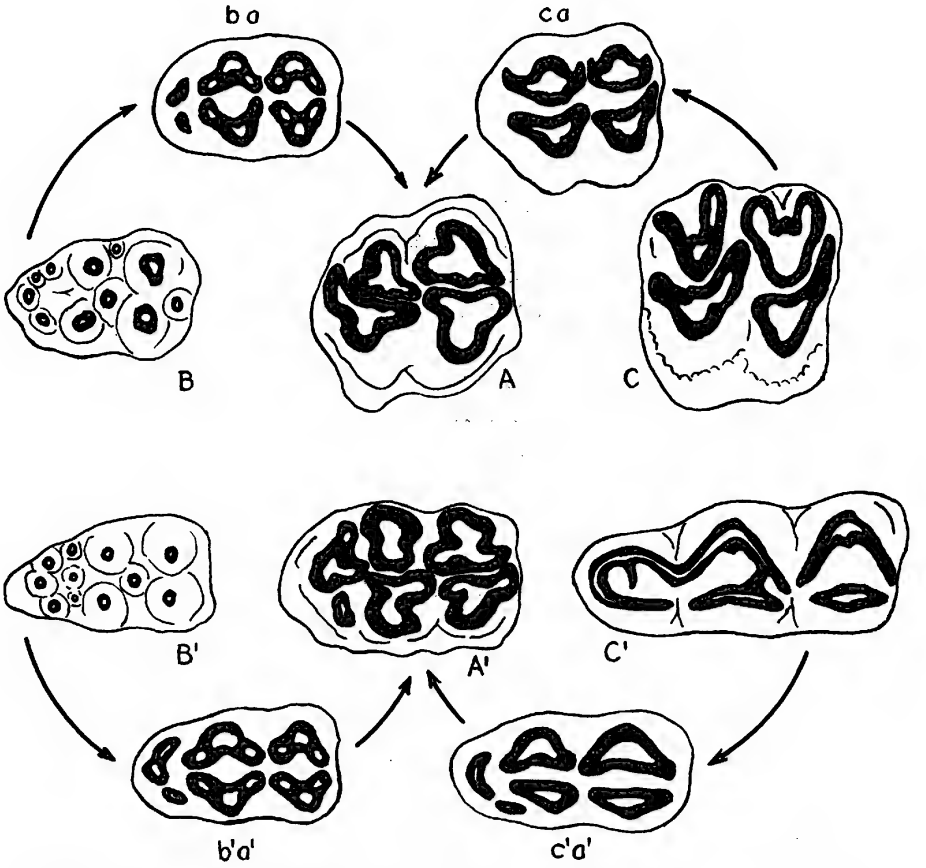

Fig. 2. The origin and evolution of the tooth pattern in the Hippopotamidae.

A, A′. Upper and lower third molars of *Hexaprotodon sivalensis.*

B, B′. Upper and lower third molars of *Conohyus sindiense.*

C, C′. Upper and lower third molars of *Merycopotamus dissimilis.*

ba, b′a′. Hypothetical intermediate stages between the Suidae and the Hippopotamidae.

ca, c′a′. Hypothetical intermediate stages between the Anthracotheriidae and the Hippopotamidae.

From Falconer and Cautley, Forster Cooper and Pilgrim. Figures not to scale.

chosen as an anthracothere approximating to a considerable extent the type that might have been ancestral to the Hippopotamidae. Really primitive hippopotami are not known, a fact the significance of which will be pointed out below, so it becomes necessary to use a form not greatly different from the modern *Hippopotamus*. *Hexaprotodon*, from the Siwaliks, is chosen, because it is slightly more primitive than *Hippopotamus*, and because it is known from adequate material.

On the left side of the chart are shown the steps involved in the transformation of a primitive suid molar into an *Hippopotamus* molar. This change involves the concrescence of accessory conules with the primary cones, to form trefoils, and in addition, a distinct shortening of the tooth.

On the right side of the chart are shown the steps involved in the transformation of an advanced anthracothere molar into a *Hippopotamus* molar. This change involves in the upper molars the expansion of the "barrels" of the paracone and the metacone and the suppression of the inner crescents of these two cusps, and concomitantly a buccal growth of the inner portion of the protocone and of the metaconule. In the lower molars there would have been a lingual growth of the protoconid, metaconid, entoconid, and hypoconid.

Considering now the premolar teeth, we see that the *Hippopotamus*, anthracothere, and suid premolars are all very much alike. In the last upper premolar of the Suidae, however, there are two outer cusps and one internal cusp, whereas in the Hippopotamidae and the Anthracotheriidae there is but one outer cusp. In some of the anthracotheres, especially such genera as *Gelasmodon* or *Merycopotamus*, the lower premolars are strikingly similar to those in *Hippopotamus*.

The Hippopotamidae and the Anthracotheriidae are characterized by their vertically directed canines, whereas the Suidae have laterally directed canines.

B.—Skull and Mandible

In the skull and mandible there is a marked resemblance between the Hippopotamidae and some of the advanced Anthracotheriidae, such as *Merycopotamus*. The following characters are common to these two families (as expressed in the Anthracotheriidae by advanced genera).

1.—Elevation of the orbit.

2.—Position of the infraorbital foramen.

3.—Shape of the zygomatic arch.

4.—The broad, vertical occiput.

5.—The low, wide glenoid. (Secondarily raised in *Merycopotamus*.)

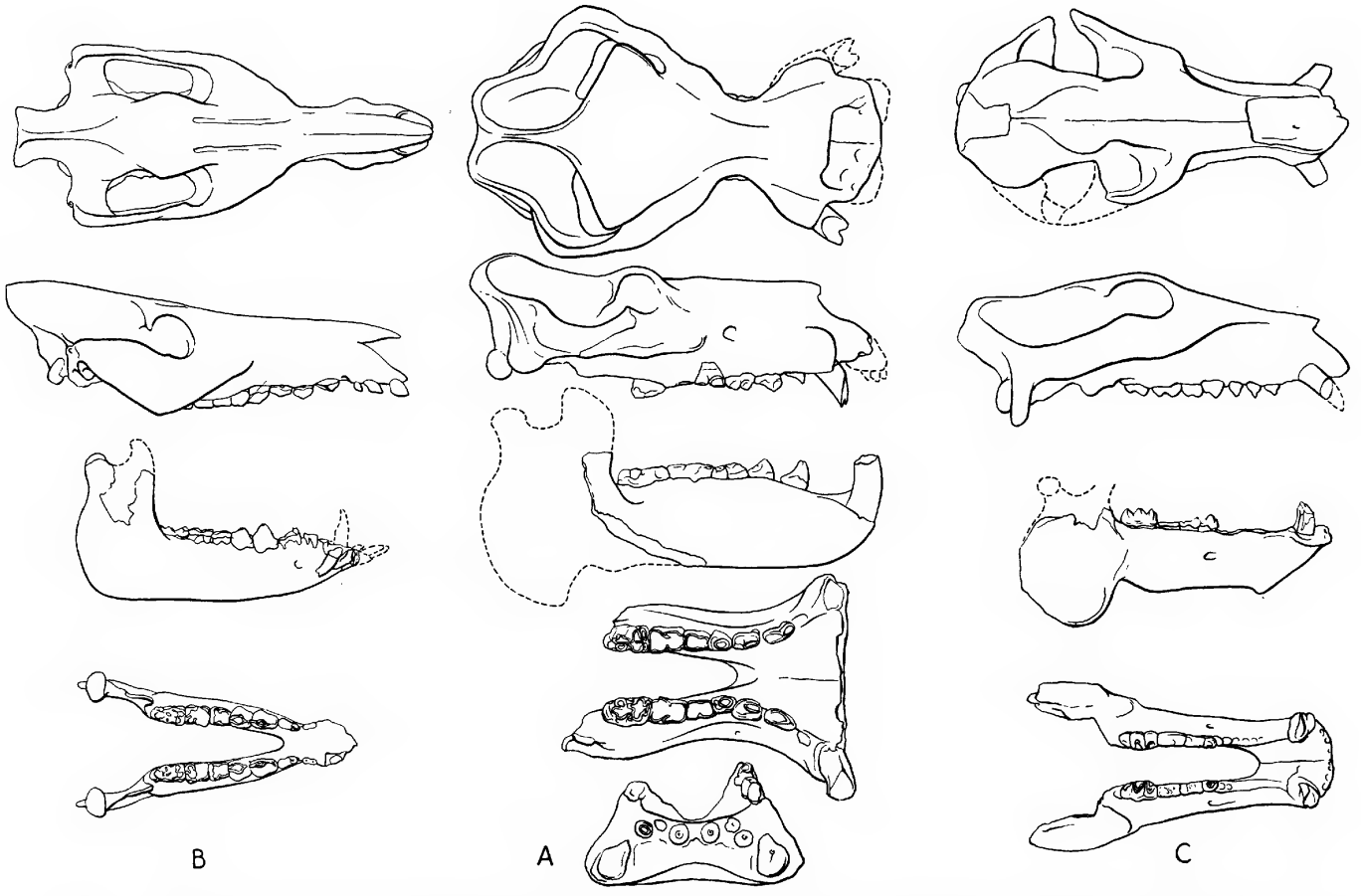

Fig. 3. Comparison of the skull and mandible in the Hippopotamidae, the Suidae, and the Anthracotheriidae. A. *Hexaprotodon sivalensis*, Upper Siwaliks. B. *Conohyus sindiense*, Lower Siwaliks. C. *Merycopotamus dissimilis*, Upper Siwaliks. The front view of the mandibular symphysis of *Hexaprotodon* is included to show the diminution in size of the second incisor.

From Falconer and Cautley, and Colbert. Figures not to scale.

6.—The short paroccipital processes.
7.—The general configuration of the auditory bulla.
8.—The postglenoid compression.
9.—The high mandibular coronoid.
10.—The deep angle of the mandible.
11.—The broad mandibular symphysis.

In comparing the *Hippopotamus* skull and mandible with those of the pig, we find the following characters common to both families.

1.—Elevation of the orbit (in certain specialized suids).
2.—The postglenoid compression.
3.—The expanded maxilla for the accommodation of the large canine.
4.—The long tube for the external auditory meatus, opening in an upward direction.

From the above it will be seen that there is a great preponderance of like skull and jaw characters in the Hippopotamidae and the Anthracotheriidae, as compared with the characters common to the Hippopotamidae and the Suidae. Of course the above lists may not be strictly diagnostic of the real resemblances and differences in these groups. Some of the above outlined characters may very well be due to parallelisms, rather than to direct genetic relationships. It seems difficult, however, to account for many of the resemblances in the skulls of the Hippopotamidae and the Anthracotheriidae as due entirely to parallel evolution. The shape of the occiput, the low glenoid, the short paroccipital processes, the auditory bulla, and the form of the mandible would seem to be characters that, when taken together, are significant of a probable relationship between the Hippopotamidae and the Anthracotheriidae.

Moreover, the entire trend of evolution in the suid skull and jaw, from the Oligocene on, is *away* from the hippopotamus habitus, whereas the trend of evolution in the anthracothere skull and jaw is seemingly *toward* the hippopotamus habitus. It may be that the numerous resemblances between the skull and jaws in the advanced anthracotheres and in *Hippopotamus* are entirely fortuitous, but, if so, they require for their explanation an unusual degree of parallelism in these two families.

In a recent number of the Journal of Anatomy, Miss H. S. Pearson[1] discusses in some detail the hinder end of the skull in *Merycopotamus* and in *Hippopotamus*. She concludes that *Merycopotamus* is a true anthracothere, and that it does not show any closer affinities to the Hippopotamidae than do any of the other anthracotheres. After a detailed consideration of the skull of *Hippopotamus minutus* she decides that the

[1]Pearson, H. S. 1929. Journal of Anatomy, LXIII, pp. 237–241.

fossil specimen is essentially similar to the modern species, and that any differentiation must needs be made on the basis of the teeth.

It may be that *Merycopotamus* is no closer in the structure of its skull to the Hippopotamidae than are any of the other anthracotheres. But the fact remains that the anthracotheres, as a group, do show many significant similarities in skull structure to the Hippopotamidae, as has been pointed out in the preceding pages.

C.—SKELETON

Coming now to the skeleton, we see that such comparisons as may be made suggest the probability of relationships between the Anthracotheriidae and the Hippopotamidae. Andrews[1] has noted the similarity in the pelves of *Brachyodus*, an anthracothere from the Fâyum deposits of Egypt, and *Hippopotamus*.

"—these animals [i. e., the anthracotheres] in many points, e.g. in the pelvis (see p. 185), approach very nearly to the Hippopotamidae, which were probably derived from them. Remains of one of the earliest and most primitive Hippopotami known, viz. *H. hipponensis*, have already been found in the Middle Pliocene of Egypt, so that there is every prospect that annectant forms between *Hippopotamus* and the Anthracotheres may be discovered in this region in deposits between the Lower Miocene and the Pliocene."

In concluding a description of the pelvis of *Brachyodus* this same author[2] makes the following remarks.

"This arrangement is also found in a very similar pelvis of *Brachyodus africanus* from Maghara and in *Hippopotamus:* this last genus, in fact, seems to be intimately related with the African Anthracotheres, and annectant forms similar to *Merycopotamus* will probably be discovered in the Miocene beds between Maghara and the Wadi Natrun, in the Lower Pliocene deposits of which remains of a primitive Hippopotamus have already been found."

In the Suidae the pelvis is narrow as compared to the pelvis in the Anthracotheriidae and the Hippopotamidae, and the ilia are not flared. Other minor differences are to be noted.

Then, in comparing the tarsus of the forms under consideration, a close resemblance is to be seen in the broad astragalus of the advanced anthracotheres and the hippopotami, whereas the astragalus in the pigs is narrow.

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[1]Andrews, C. W. 1906. 'A Descriptive Catalogue of the Tertiary Vertebrata of the Fâyum, Egypt.' London, p. xx.

[2]Andrews, C. W. 1906. *Op. cit.*, p. 186.

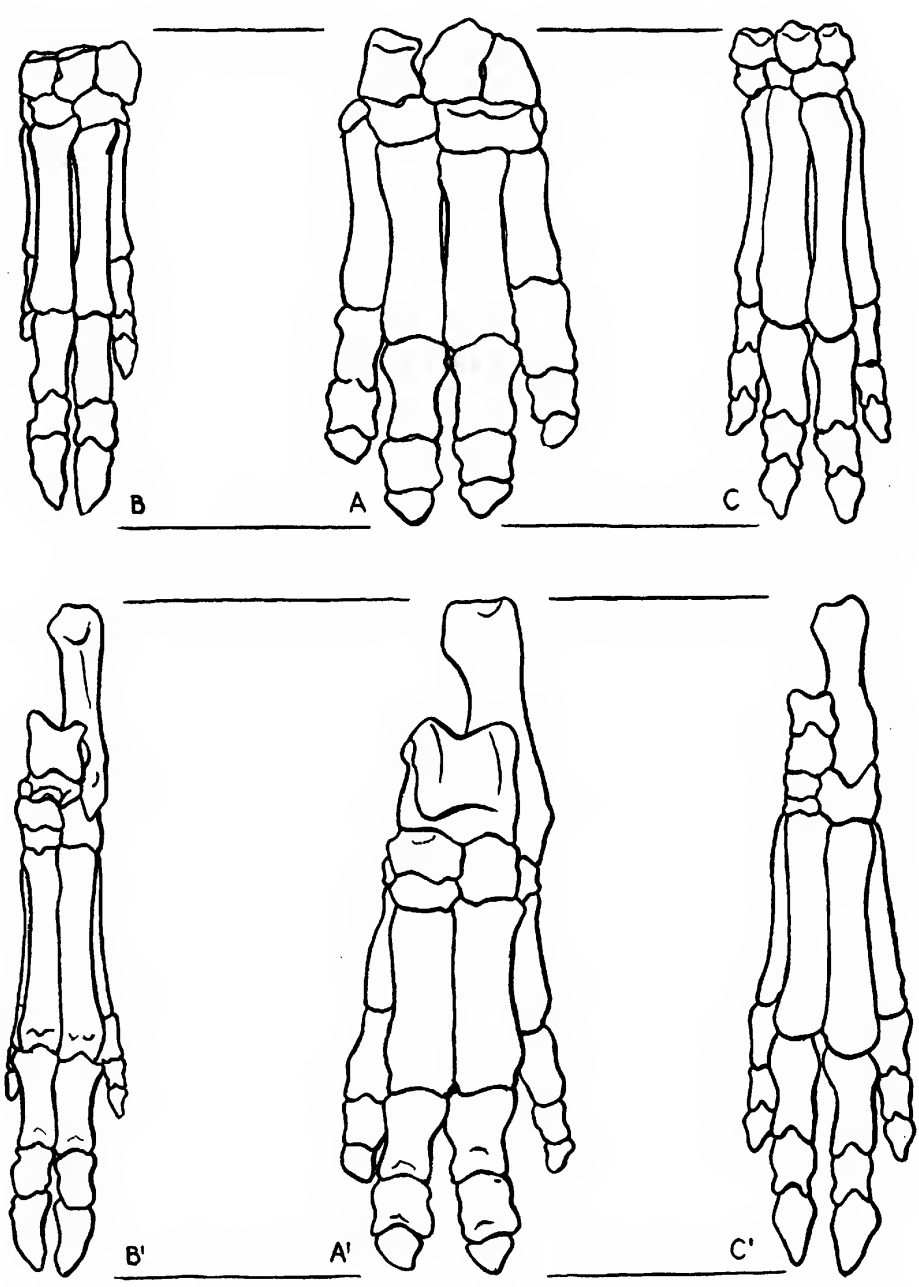


Fig. 4. Comparison of the manus and pes in the Hippopotamidae, the Suidae, and the Anthracotheriidae.

A, A′. Manus and pes of *Hippopotamus amphibius*.

B, B′. Manus and pes of *Sus scrofa*.

C, C′. Manus and pes of *Ancodus brachyrhynchus*.

From de Blainville, Scott and others. Figures not to scale.

Of course these skeletal characters may be due to the adaptations of the anthracotheres and the hippopotami to the increase in body weight, necessitating at least semi-graviportal structures, as compared to the cursorial adaptations in the suids. The fact remains, however, that the largest anthracotheres were no larger than large pigs, yet in many of their skeletal characters, notably in the pelvis and the feet, they showed a trend toward the *Hippopotamus* habitus rather than one toward the Suidae.

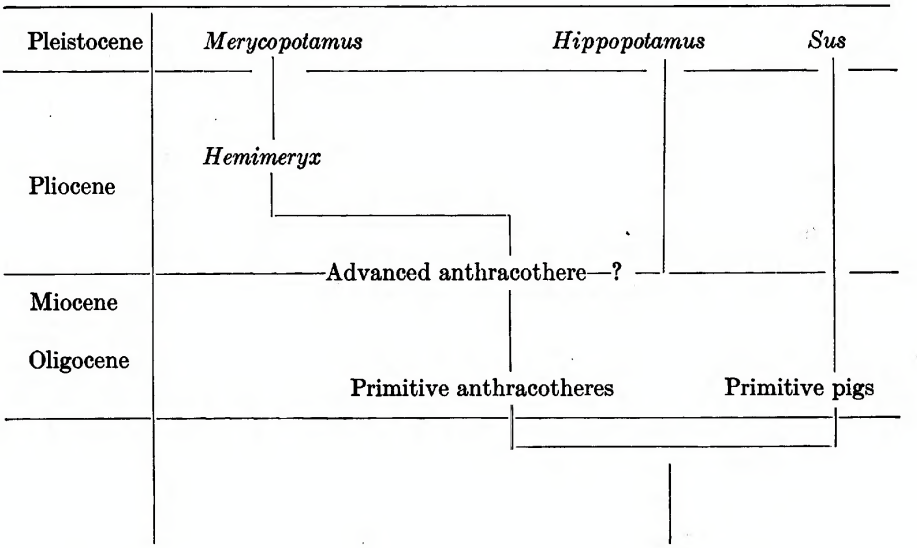
Taking the evidence all in all it will be seen that resemblances exist between the anthracotheres and the hippopotami and between the pigs and the hippopotami. It would seem to me, however, that the anthracothere-hippopotamus resemblances are certainly more numerous and probably more convincing than the pig-hippopotami resemblances. A definite and a final solution of this vexing problem of the origin of the Hippopotamidae is difficult to reach, because the evidence is peculiarly suited to factors of individual interpretation. The most primitive Hippopotamidae known are not appreciably different from the modern forms. Thus it becomes necessary to use many advanced, specialized habitus characters in drawing our comparisons, and these tend to mask, or rather to crowd out, the more significant primitive heritage characters, the characters on which phylogenetic ties between groups must ultimately rest.

I have attempted to show in the above remarks that the trend of evolution has been similar in the Anthracotheriidae and the Hippopotamidae, whereas the evolutionary trend in the Suidae has been on the whole quite unlike the trend in the Hippopotamidae.

Furthermore, it seems to me that Andrews made an unusually sagacious remark when he said "that there is every prospect that annectant forms between *Hippopotamus* and the Anthracotheres may be discovered in this region [Egypt] in deposits between the Lower Miocene and the Pliocene." We do not know any primitive Hippopotamidae from the earlier portion of the Tertiary. May not this be due to the fact that the Hippopotamidae is a family of late evolutionary development, a family that broke away from its ancestral group in the late Miocene? It may be that primitive, early Tertiary Hippopotamidae have never been found because such animals never existed.

If the Hippopotamidae did break away from an ancestral stem in the late Miocene, what might this stem have been? Certainly not the pigs, which by that time had become set in an evolutionary trend quite away from the *Hippopotamus*-type of structure. Why not, therefore,

the anthracotheres, which in the Upper Tertiary show numerous structural characters strongly suggestive of the Hippopotamidae? Perhaps the great similarity of *Merycopotamus* to *Hippopotamus* is due to the fact that the former is not far removed from the *advanced* anthracothere type, from which the latter may have been derived. This suggestion may be represented diagrammatically as follows.



In the above discussions the arrangement of the basicranial foramina in the Anthracotheriidae, the Suidae, and the Hippopotamidae was not utilized for comparisons, because of the similarities existing among the advanced forms of the first two families and of the Hippopotamidae. In all of these families the foramina are coalesced around the bulla, a common character in the more specialized artiodactyls.

Was *Cebochoerus* Ancestral to the Hippopotamidae?

Miss H. S. Pearson has suggested that the Hippopotamidae may have been derived from *Cebochoerus* of the Eocene of Europe. She bases her argument on the following characters common to or similar in both groups.

1.—The shape of the glenoid.
2.—The position of the glenoid.
3.—The position of the post-tympanic, anterolateral to the paroccipital.

Although there are resemblances between *Cebochoerus* and the Hippopotamidae in the above-mentioned characters, many differences, which it seems to me are of greater importance, may be found. The skull and the dentition especially, of *Cebochoerus*, are specialized along a quite definite trend, not toward the Hippopotamidae, but rather in a direction of their own.

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